

## chapter 1

# THE TIME SCALE AND SOME EVOLUTIONARY PRINCIPLES

To most of us, paleontology is the name of a sort of genteel outdoor science concerned with the collection and gross description of old bones and hardened mud blocks containing preserved animal tracks. To the paleontologist and, for that matter, to any novice who has had the good fortune to pass through what might be called the "Darwin-to-Simpson reading stage," no definition could be further from the truth. Just as history, to the historian, is alive and a part of the continuing pageant of human experience, so is the study of the life of the past a living science to its devotees.

The study of fossils cannot tell us a great deal about the natural forces that shape the evolutionary process, but it does furnish us with guidelines for the consideration of information derived from other sciences. As G. S. Carter<sup>1</sup> has put it, "The part of paleontology in the study of evolutionary theory resembles that of natural selection in the process of evolution; it serves to remove the inefficient but cannot itself initiate." It is clear that we can, and should, present only the most superficial survey of the fossil record and its interpre-

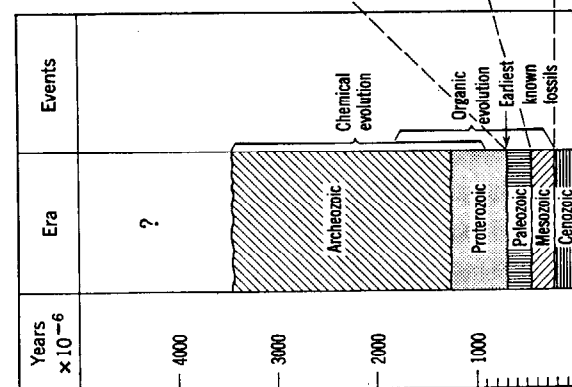


Figure 1. Time scales for the earth and for life on the earth.

tation in the present volume. For our purposes here we need only arrive at some general appreciation of the arbitrary divisions of geological time and outline the phylogenetic relationships that exist between the various living and extinct forms of life.

Measurements of the extent of decay of long-lived radioactive elements in the rock strata of the earth's crust enable us to make reasonable estimates of the ages of various strata. Utilizing such data as check points, but relying mostly on time estimates arrived at by classical geological methods, the paleontologist can arrange the fossilized remnants of life in a consecutive order with reasonable accuracy. He can also, in many cases, make certain deductions concerning the relation of specific upheavals and rearrangements of the earth's surface to the changing patterns in the nature and distribution of life as it was in the past.

For the purposes of those interested in the earth sciences, time may be expressed perfectly well on a linear scale, as shown on the left of Figure 1. Such a scale serves to emphasize the relatively small fraction of global time during which life has existed on the earth. The biologist is, however, more naturally preoccupied with "protoplasmic" time and must magnify the portion of the time scale that has to do with living things. The right half of Figure 1 is more useful to the biologist and lists some of the landmarks in evolution, assigned to their proper paleontological time period.

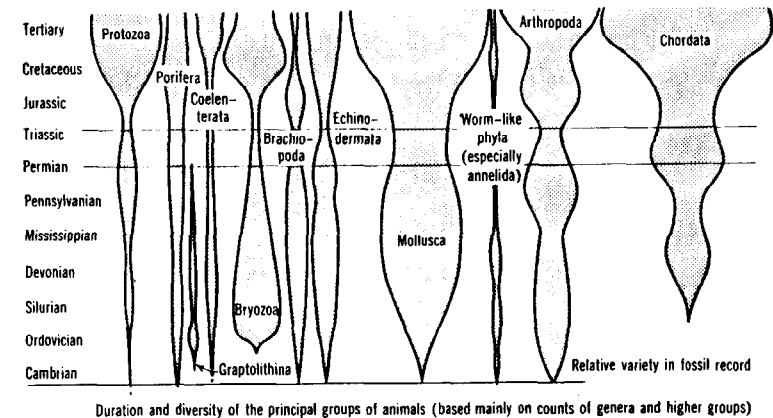
The earliest fossils that occur in any abundance may be assigned to the Cambrian and Ordovician periods and include a large proportion of the basic types of aquatic animals and the possible beginnings of the vertebrates. The record for the Pre-Cambrian period is extremely sparse and is represented mostly by the relatively primitive plants, the algae. At the end of the Pre-Cambrian, most of the invertebrate phyla were relatively well differentiated, although the absence in most instances of structural elements that could survive as fossils makes the reconstruction of their phylogenetic tree somewhat controversial. One scheme is presented in Figure 2. This arrangement of the phyla, which includes the higher vertebrate forms for comparison is, according to its author, L. H. Hyman, not to be taken literally but is only suggestive. It is based on an arrangement of animals in order of structural complexity, without separation of the allied phyla. The bacteria, yeasts, etc., are not shown, for they branched off at some early point in time when the momentous biological accident occurred which led to the establishment of plant and animal kingdoms.

Another way of looking at the phyla is shown in Figure 3, taken

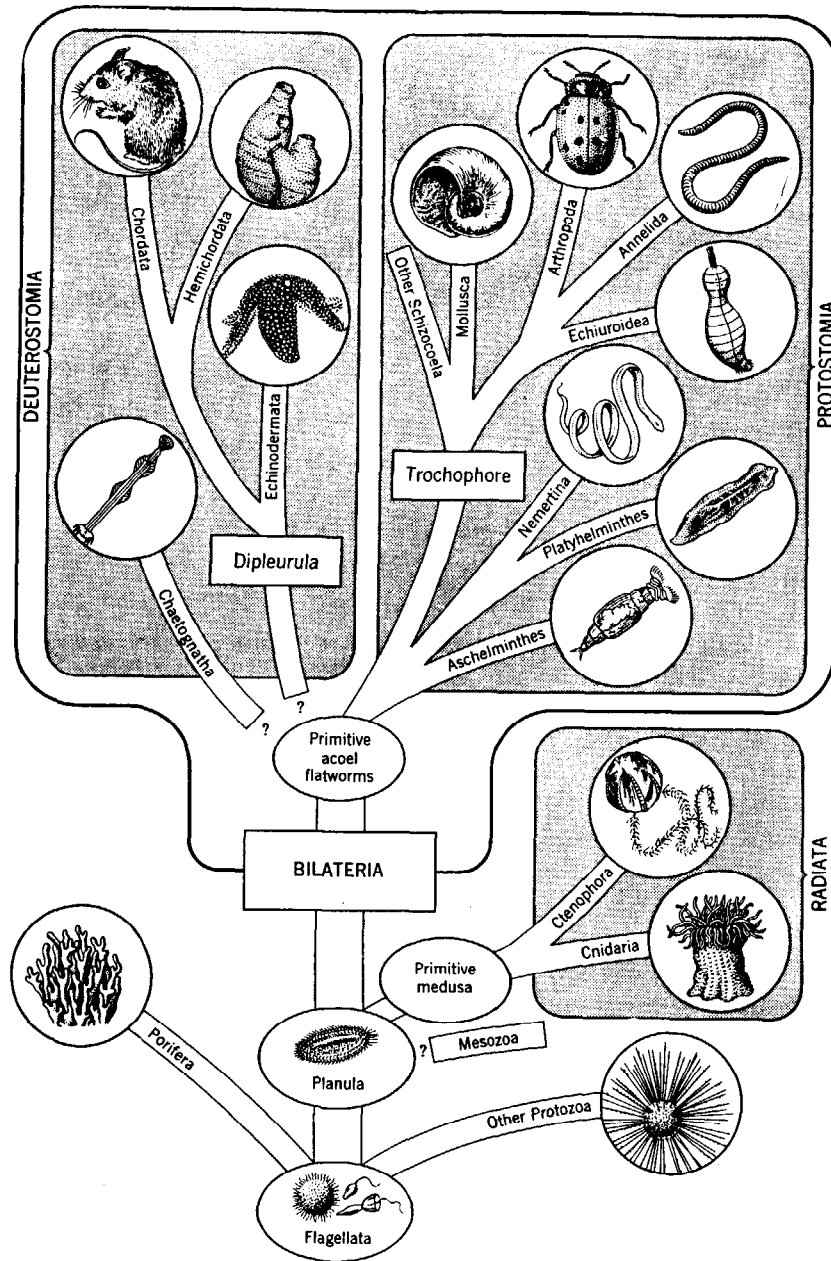
from George Gaylord Simpson's fascinating book, *The Meaning of Evolution*. Here we see the major phyla, as they have existed through most of biological time, in terms of their relative abundances. We can observe here some of the correlations between geology and biology which the paleontologist is able to make. For example, the distinct contractions in the abundances of almost all the phyla in the Permian and Triassic periods and the actual extinction of the Graptolithina correlate well with the geological evidence for great mountain building and climatic rigor during these times.

A final illustration for this phylogenetic orientation is given in Figure 4, in which the vertebrates are arranged in their proper ascendancy (to use an "anthropophilic" expression). In our discussions of the relations between the biochemistry and genetics of various organisms we shall refer from time to time to the contents of these figures. We shall be interested, for example, in the structure of proteins as they occur in various species and in the possibilities of making some crude estimates from such data of the rates at which specific genes have become modified.

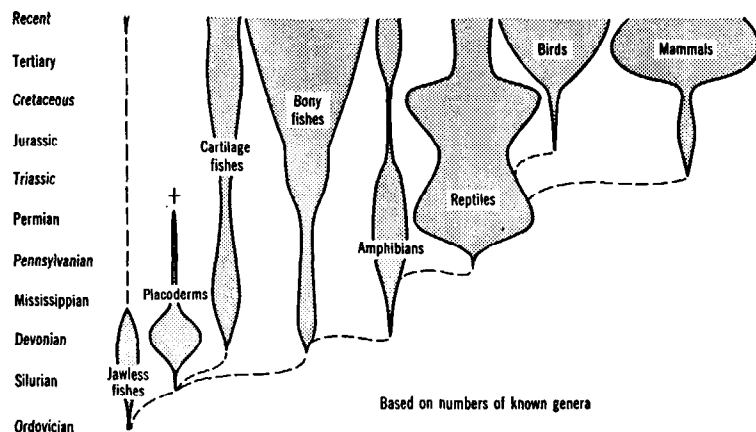
The basic characteristics of the evolutionary process vary considerably, depending on the level of evolution which is being considered. Evolutionary change, measured broadly in terms of the origin of new systems of animal organization, is an expression of *average* change.



**Figure 3.** A schematic diagram of the history of life. The various phyla of animals are represented by paths, the widths of which are proportional to the known variety of each phylum during the various biological periods. Redrawn from G. G. Simpson, *The Meaning of Evolution*, 1950, by permission of Yale University Press.



**Figure 2.** Relationships of the phyla of the animal kingdom. The arrangement here is based on the scheme given by L. H. Hyman in *The Invertebrates*, volume 1, McGraw-Hill Book Company, p. 38, 1940.



**Figure 4.** A schematic diagram of the history of the vertebrates. The widths of the pattern for each vertebrate class is proportional to the known varieties of the class in each of the geological periods. Redrawn from G. G. Simpson, *The Meaning of Evolution*, 1950, by permission of Yale University Press.

As Simpson has put it, "It is populations, not individuals, that evolve." As we approach the level of immediate cause and effect, however, certain aspects of evolution become more highly significant, and when we consider a small experimental population of the fruit fly, *Drosophila*, we must become more concerned with individual mutations and their contribution to the survival or death of these specific flies than with theoretical, infinitely large populations. This example is obviously not evolution in the grand sense. It emphasizes "the survival of the fittest," a phrase which, in the light of modern ideas, we know must be replaced with "the survival of the branch of a population which is adapted well enough to its environment to live to procreate." Nevertheless, all evolutionists will agree that the basic cause of change must be gene mutation (although some authors will hold out for the additional involvement of something more ethereal in the way of causation, variously termed "aristogenesis," "élan vital," "entelechy," among other names—we shall return briefly to these terms later in this chapter).

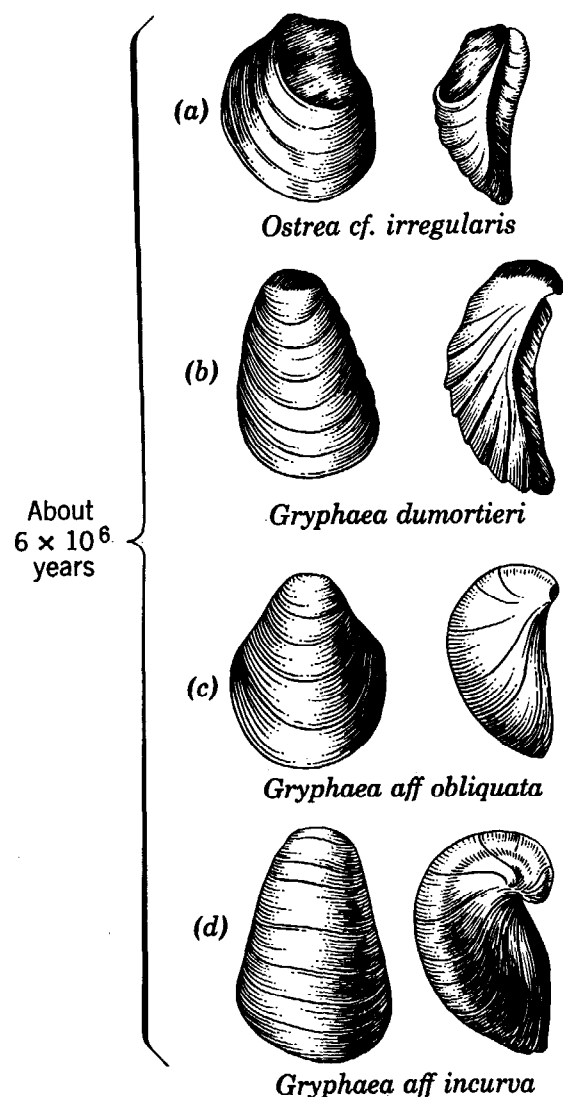
As our store of information concerning species variations in biochemical properties, and specifically in protein structure, increases, we will do well to have before us, as a constant frame of reference, a clear picture of the phylogenetic relationships between various forms of life and, particularly, of the time, in terms of numbers of generations, required to accomplish these variations.

To develop some appreciation of the magnitude of time involved in the differentiation of a species in relation to that required for a more sweeping phylogenetic change, let us briefly examine those divisions of the process called micro-, macro-, and megaevolution. To quote the capsule summary given by Carter,<sup>1</sup> "There is, first, the origin of the smallest evolutionary differences as seen in continuous series of strata; secondly, there is the differentiation of the members of a group in adaptive radiation; and thirdly, the evolution of a new type of animal organization from its predecessors."

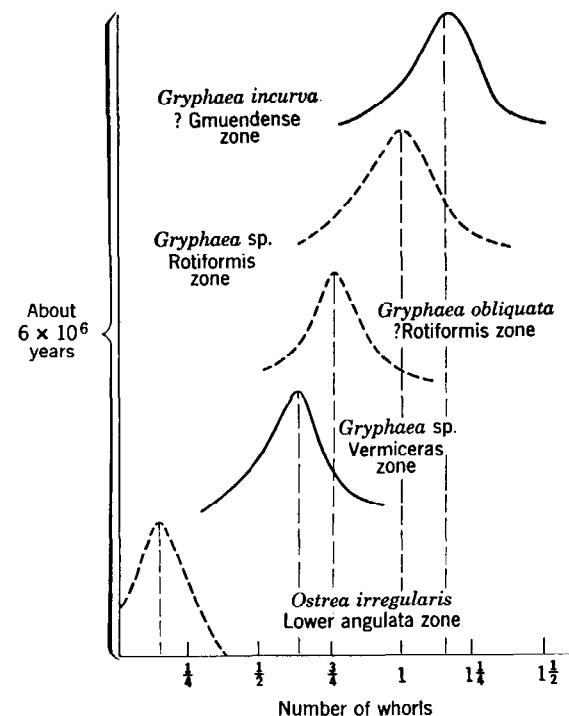
### Microevolution

In certain favorable instances, when geological processes have resulted in the formation of a continuous local succession of strata, paleontologists have been able to reconstruct the morphological progression of a species as it took place over many hundreds of thousands of years. An elegant example of such a reconstruction is the work of Trueman<sup>2</sup> and his collaborators on the evolution of the coiled lamellibranch, *Gryphaea*, a mollusk derived from oysters of the genus *Ostrea* which is frequently found in the strata of the Mesozoic era. Mollusks of the genus *Gryphaea* arose frequently and independently from flat-shelled predecessors, presumably in response to the necessity for raising the mouth of the shell above its muddy environment. Four stages in the progressive development of a line of *Gryphaea* are shown in Figure 5. During the evolution from *Ostrea irregularis* to *Gryphaea incurva* a number of morphological characters were modified, and each of these was changed at different rates. Any one of these characters may be used as a measure of rate of change; in Figure 6 is shown a plot of the variations in one of these, the number of whorls in the shell, as a function of the vertical location of the sample studied within the superimposed strata. The populations examined by Trueman from any given stratum gave a unimodal distribution curve, strongly suggesting that the population was single and was not a mixture of independent populations.

In a case such as this there is little question that microevolution has occurred without any large and sudden changes (saltations). The general characteristics of the evolution typified by the *Gryphaea*, with its succession of imperceptible gradations and with its uniformity around a mean, led Trueman to suggest that "such an evolving stock must be regarded as a 'plexus' or 'bundle of anastomosing lineages.'" The example has been presented here mainly to illustrate



**Figure 5.** Four stages in the evolution of *Gryphaea* from its oyster-like ancestor. Redrawn from A. E. Trueman, *Biol. Revs. Biol. Proc., Cambridge Phil. Soc.*, 5, 296 (1930).



**Figure 6.** Distribution curves showing the variation in the number of whorls of the shells of successive populations of evolving *Gryphaea*. Redrawn from A. E. Trueman, *Biol. Revs. Biol. Proc. Cambridge Phil. Soc.*, 5, 296 (1930).

that microevolution is a population phenomenon and that the separate development of radiating lines becomes almost impossible in a restricted population since continual interbreeding prevents the successful rise of deviant groups.

### Macro- and Megaevolution

When a mutation confers some benefit on an organism within the framework of the environmental restrictions on the population to which it belongs, the characteristic controlled by the mutant gene may ultimately become firmly entrenched in the heredity of the entire group. However, a limited horizon, such as that available to the *Gryphaea*, permits only a limited phenotypic change. Thus, even though a few "advanced" *Gryphaea* might have appeared which were

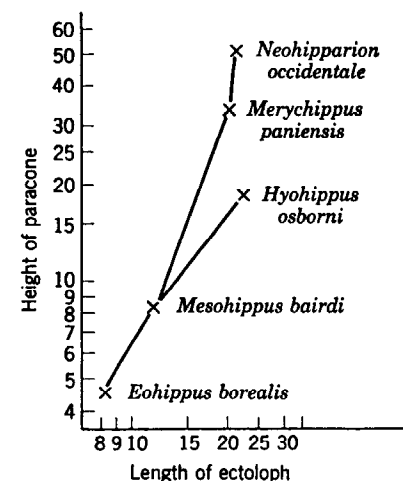
endowed with some unique and specially favorable character, they would not be likely to be perpetuated as a unique strain because of their random interbreeding with the standard average organism.

The major factor responsible for the larger changes in evolution that lead to distinct new specializations, or to new systems of animal or plant organization, is *adaptive radiation*. Adaptive radiation is the term used by evolutionists to describe the separation of populations into smaller groups having different natural histories. The more mobile the group and the more demanding the environmental changes to which adaptation must be made, the greater the diversity of form (and the number of unsuccessful "experiments") that results. This diversity and mobility, together with the concomitant high rate of evolutionary change, make the fossil record scattered and incomplete as opposed to the situation for the sedentary *Gryphaea*. Nevertheless, paleontologists have been able to reconstruct the phylogeny of numerous lines with great success, and certain distinct parameters of macroevolution are well delineated.

The macroevolution of a particular population of organisms leads to great complexity of form, most of the examples of which are false starts and become extinct after a relatively short time (paleontologically speaking). For an evolutionary development to be successful, all the various morphological parts must change in a correlated way to insure survival. The evolutionists can express such correlations in relative growth and development of parts by means of double logarithmic plots, as shown in Figure 7. Here are represented the relations between the heights of the paracones (a cusp of the molar teeth) and the lengths of the ectolophs (the ridge on the outer border of the crown of the same tooth) of the teeth of horses during their progression from the primitive *Eohippus* to the modern animal. Characters that may be related by such straight-line plots (of the general form  $Y = bX^k$ ) are said to be undergoing allometric change, and the slopes of the lines ( $k$ ) give a measure of the relative rates at which two specific bodily characters are changing.

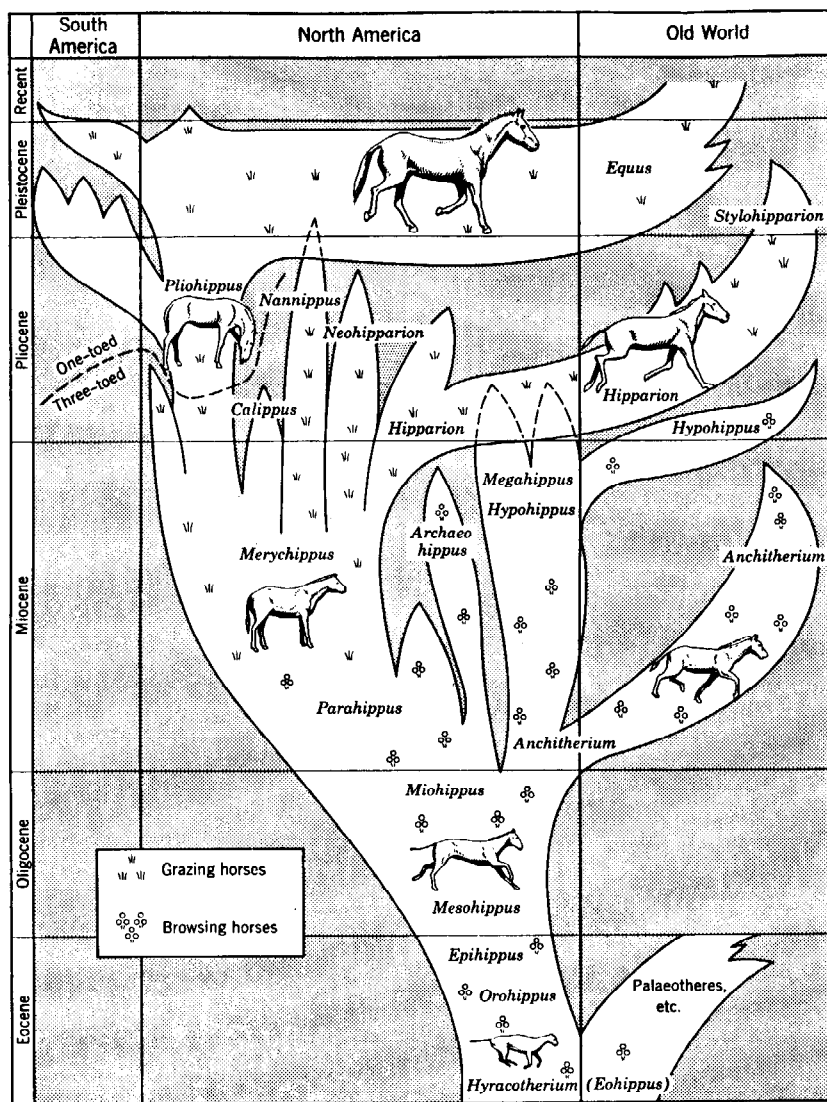
A sudden modification in the slope of the plot relating two allometric changes indicates a sudden shift in evolutionary direction. For example, such an indication is given several times during the evolution of the horse. As horses underwent adaptive radiation they became exposed to new types of environmental opportunities involving both new kinds of food and new terrain. The changes in the position of the eye and in the structure of the foot and of other physical characteristics have been described in a fascinating way by Simpson in his book *Horses*. The modification of the molars

Figure 7. Changes in the structure of the molars during the evolution of the horses. After G. G. Simpson, *Tempo and Mode in Evolution*, 1944, by permission of Columbia University Press.



during equine evolution is particularly instructive in connection with our present consideration of sharp changes in evolutionary direction. As ecological conditions made browsing more favorable than grazing, the whole plan of the molar was modified by natural selection in a direction compatible with the abrasive action of hard grasses. Thus the crown of the molar became thicker and, together with the development of cement, permitted the animals to enjoy a fertile life span in spite of the erosive nature of their natural food supply. A schematic representation of the adaptive radiation of horses is shown in Figure 8. This figure shows the eating habits of the various successive members on the main evolutionary line. The correlative plot of two allometric structural features of the molars, the size of the tooth and its height, shows that there occurred an abrupt increase in the relative height of the tooth in the horses that converted to grazing, whereas in another evolutionary offshoot, *Hyohippus*, which continued to browse on soft, easily chewed plants, such a change did not occur.

Most authorities seem to agree that the evolution of a particular line of organisms, like the horses, can be explained without complication on the basis of the selection of mutants that confer a survival value on the individual and on the population to which he belongs. The occurrence of a particularly advantageous mutation has frequently led to an almost explosive change in structure or habit, and Simpson has proposed the name "quantum evolution" for such major jumps. The view is frequently expressed, however, that the process of natural selection might still be an adequate explanation for these rapid shifts. Their suddenness is perhaps overemphasized because



**Figure 8.** The evolution of the horses. The diagram shows the geographic distribution of the various forms and indicates their manner of securing food by browsing or by grazing. Redrawn from G. G. Simpson, *Horses*, 1951, by permission of Oxford University Press.

of gaps in the fossil record that resulted from the rapidity of the changes and the limited geographical region in which they occurred.

In discussions of those portions of evolution in which whole new systems of biological organization arose, the terminology and interpretations of experts becomes varied and, sometimes, delightfully mystical, at least to window-shoppers such as myself. We have already mentioned the terms *entelechy*, *élan vital*, and *aristogenesis*. Such terms have been coined to explain (explain away, perhaps) the frequent, puzzling phenomena in which new structures and physiologies have arisen in the absence of obvious adaptive value or selective influence. During the evolution of reptiles, for example, there occurred a simplification of the jaw structure which made superfluous the quadrate and articular bones of the reptilian jaw. Ultimately, millions of years later, these "liberated" units became involved in a major change in the structure of the middle ear and made possible the chain of small bones which is characteristic of this organ in mammals. This "aristogenic" change, leading to an entirely new anatomical organization at a much later time, is not easy to explain on the basis of selection and adaptation alone. The phenomenon has implied to some that the evolutionary process has, built into it, some knowledge of the future and that temporarily useless structures may be stored away for later use according to some master plan.

From the standpoint of maintaining a more unified picture of the evolutionary process, "aristogenesis" and the "preadaptation" of an organism for some subsequent evolutionary event do not appear to be necessary concepts. Simpson has pointed out that, in small populations, a mutation which confers no adaptive value (or, indeed, which may be detrimental) *can* become established, although "almost always this would lead to extinction." In those rare cases when the word "almost" applies, a change in the natural history of the organism might then cause an enormously rapid and major evolutionary modification owing to the sudden usefulness of this otherwise disadvantageous gene, fortuitously harbored in the heredity of the strain. From this point of view we may explain the whole of evolution, from the localized, sedentary sort of microevolution to the dramatic appearance of new phyla, on the basis of mutation and selection alone.

As we shall discuss in a later chapter, certain structural parts of biologically active proteins appear to be superfluous from the standpoint of function. A tendency to assume that such parts are non-essential might simply reflect the fact that we have not yet developed sufficiently sensitive methods for the detection of subtle, second-order relationships between structure and function. On the other hand,

certain structural configurations may now actually *be* unessential and may have been preserved as chemical vestiges of earlier molecules, much as the bones of the mammalian ear were retained from the rearranging components of the reptilian jaw.

The information available to us on proteins and other chemical components of protoplasm is, of course, insufficient to permit a rational choice between these alternatives at the present time. We can only hope, in analogy to the paleontologist and his "fossil record," that as the "protein record" relating the proteins of various species to one another becomes more complete, some basic ground plan for phylogenesis and speciation may begin to emerge at a molecular level of understanding.

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